NEST PREDATION IN RIPARIAN BUFFER STRIPS IN A BALSAM FIR FOREST IN WESTERN NEWFOUNDLAND

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Nest Predation in Riparian Buffer Strips in a Balsam Fir Forest in Western Newfoundland

by

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A thesis submitted to the School of Graduate Studies in partial fulfillment of the requirements for the degree of Master of Science

Biopsychology Programme

Memorial University of Newfoundland

January 1999

St. John's Newfoundland

Abstract

Logging pressures on boreal forests have increased in recent decades and carry with them increased concerns for wildlife and habitat conservation. Buffer strips mitigate some of the negative impacts of logging on riparian habitat and associated wildlife. Given the widespread use of buffer strips, the subsequent increase of clear-cut/forest edge, and the decline of many forest birds, I investigated how buffer strips and habitat edges influence avian nesting success. Nest predation is the most common cause of nest failure among song birds. Therefore, artificial nests are a useful research tool for investigating the influences of habitat alteration on nest predation. Japanese Quail (*Coturnix japonica*) eggs are often used in artificial nest studies, although these eggs may be too large to detect predation by small mammals. My primary objectives were to determine 1) if nest predation differs between intact riparian forest and a) buffer strips and b) clear-cut forest edges, and 2) if Japanese Quail eggs are appropriate to use in artificial nest studies in western Newfoundland.

Artificial tree and ground nests (n = 150 in 1996, n = 420 in 1997) with Japanese Quail eggs were used to measure nest predation in study blocks (k = 5 in 1996, k = 7 in 1997) that included buffer strips, intact riparian forest, and clear-cut forest edges. The second experiment used artificial ground nests (n= 180) with Chinese Painted Quail (*Xexcalfactoria chinensis*) eggs and Japanese Quail eggs to measure the influence of egg-size on ground-nest predation in buffer strips (k = 4)

and intact forest sites (k = 5). The influences of buffer strip width, nest visibility, and distance of the nest from the nearest edge on nest predation were measured and nest predators documented.

Nest predation was significantly different and extremely variable between study sites in both experiments suggesting that local presence of predators may be influenced by site-specific conditions, rather than specific types of habitat alteration. Nest predation did not differ between intact riparian forest (55 %) and a) buffer strips (41 %) and b) clear-cut forest edge (50 %). Nest predation significantly increased with increasing buffer strip width (13-38 m). However, the conservation value of buffer strips is likely to increase with width due to low increases in predation, greater abundance of Neotropical migrants, and lower proportional windfall rates in wider buffer strips. Nest predation was higher on tree nests than on ground nest in both years, and nests with greater visibility were more successful than exposed nests. Gray Jays (*Perisoreus canadensis*) and red squirrels (*Tamiasciurus hudsonicus*) were the only identified nest predators. Gray Jays preyed significantly more on tree nests than ground nests while red squirrels preyed equally on both nest types. Egg-size did not influence predation. I conclude that predation is influenced by site-specific factors and that Japanese Quail eggs are appropriate for artificial nest studies in western Newfoundland.

Acknowledgments

Many individuals contributed directly and indirectly to this research. First, I would like to thank my committee for their encouragement, advice and support. My supervisor Bill Montevecchi was a source of constant support and encouragement. Ian Warkentin and Allan Carrol provided many useful comments without which this project would not have been a success.

A special thanks to Darroch Whitaker for inspiring this project, giving me a model to follow, teaching me the bird songs of the boreal forest, and for all the help in the field. This thesis is a follow up of his studies on avian assemblages in balsam fir forests.

Elaine Goudie and Todd Reid were both excellent field assistants. Their willingness to put in long hours, in difficult terrain and weather conditions made this project enjoyable and a success. Both taught me a great deal of boreal flora. Lori Dillon helped measure quail eggs for the second part of this study. Jim McCarthy and Jerome Benoit were helpful in several field situations.

Len Moores and the Newfoundland and Labrador Division of Forestry provided funding and technical support for field work. Gordon Fifield was very helpful with aerial photographs and along with Dave Delany, helped with logistics. Joe Brazil and the Newfoundland and Labrador Division of Wildlife provided funding for field assistants. Logistical support was also received from the Department of Fisheries and Oceans through David Scruton. The

Departments of Biology and Psychology and the School of Graduate Studies also provided support.

Kathleen Nichols and the Quail Genetic Research Center, University of British Columbia provided the large quantity of quail eggs used in this study in a prompt, professional, and friendly manner.

Many individuals contributed to other aspects of this study. I benefitted from discussions with Ross Mays and also from Ian Stenhouse who contributed a great deal to my knowledge of birds and reviewed the manuscript. To David Schneider, I owe most of what I know of statistics and for reminding me that statistics are just a tool for analyzing biological phenomena. Alexander Bochdansky helped with the study design and field methods. Steve Bettles helped with this too, and along with Kelly Moret, saved me weeks of time by helping me with various software packages. Mark Hipfner provided useful advice concerning egg volume. Dan Anderson and Sebastion Herzog were important influences on me as an undergraduate.

My family has been an important inspiration to me, and their example and hard work has made it possible for me to pursue an academic career. Finally, I would like to thank the Moret family for taking me into their home and family, and for their assistance in the last year.

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JQE Japanese Quail egg

CQE Chinese Painted Quail egg

Chapter 1. Introduction

1.1 Riparian Ecology

The importance of riparian ecosystems, defined as land bordering bodies of water (Small and Johnson 1985, Stocek 1994), has attracted a great deal of attention in the last three decades (e.g. Thomas et al. 1979, Small and Johnson 1985, Knopf et al. 1988, Knopf and Samson 1994, Singleton et al. 1994, Scruton et al. 1995). Riparian habitat has been found to have special ecological significance, acting as deer yards, travel corridors, or in supporting increased biodiversity (Small and Johnson 1985). In some regions, wildlife use riparian habitat more than any other type of habitat (Thomas et al. 1979). Riparian habitat is often disproportionately important to wildlife because of edge effects at riparian ecotones, increased vertical vegetative structure, greater productivity due to nutrient inputs, and horizontal diversity due to the presence of water and upland ecosystems (LaRue et al. 1995). Riparian areas are also used for forestry, grazing, farming, flood control and recreation (Thomas et al. 1979). Due to these conflicts, research has focused on how human activities affect riparian habitat (Hooper 1989).

Between 1978-88, most studies of wildlife in riparian habitat in North America were conducted west of the Mississippi River. A likely reason for the regional imbalance in research effort is the difference in the riparian systems of eastern and western North America (Hooper 1989). Riparian habitat in the

southwestern United States is rare, comprising 1 % of the total land area (Knopf and Samson 1994) which contrasts sharply with drier non-riparian habitat (Hooper 1989). Despite comprising a small percentage of the total land area, riparian areas provide habitat for more species of breeding birds than any other type of habitat in the Southwest, West, Midwest, Northwest, and Great Plains regions of the United States (Knopf and Samson 1994). In contrast, riparian habitat in eastern North America is more extensive, and the boundaries between riparian habitats and adjacent forest are less distinct (Murray and Staufer 1995). Assessing the importance of riparian habitats for terrestrial wildlife in boreal ecosystems has been more speculative (Hooper 1989). In Newfoundland, policy recommendations relating to riparian habitat management have been based on "best available information" (Scruton et al 1995).

Since Hooper's (1989) review, more studies comparing song bird richness and abundance in riparian forests with other habitats have been conducted in eastern North America (e.g. Gates and Giffen 1991, Murray and Stauffer 1995) with an increasing number of studies in eastern boreal forests. In Quebec, LaRue et al. (1995) found that avian richness was higher in riparian areas compared to interior forests. In Newfoundland, by contrast, avian richness and abundance was not higher in riparian habitat compared to interior forest, although certain species are positively and exclusively associated with riparian habitat (Whitaker and Montevecchi 1997).

1.2 Riparian and Avian Conservation

1.2.1 Riparian buffer strips

A common method of protecting riparian habitat from timber harvesting (or other forms of disturbance) is to leave a strip of undisturbed vegetation beside a waterway known as a riparian buffer strip (Small and Johnson 1985). Buffer strips have been shown to help maintain bank stability, minimize sediment inputs to waterways, provide shade and cooler water temperatures for fishes, and provide habitat for terrestrial insects (Hopper 1989, LaRue et al. 1995). Throughout North America, legislation designed to protect riparian areas requires the maintenance of buffer strips around water ways (Knopf et al. 1988). Assessing the conservation value of buffer strips is critical in Canada where 300,000-500,000 ha of forest are clear cut annually (Canadian Forest Service 1993).

1.2.2 Avian conservation

Due to the widespread use of buffer strips, their effectiveness as conservation measures is of special concern, especially in view of the extensive fragmentation of forest habitat in North America and its negative effect on breeding populations of forest birds (e.g. Robbins et al. 1989, Askins 1995, Robinson et al. 1995). Many populations of Neotropical migrants have declined

over the last 30-40 years (Sauer and Droege 1992, Robinson et al. 1995). Most species experiencing severe population declines are long-distance migrants that winter in the Neotropics and breed in North American forests (Askins 1995). Besides loss of wintering habitat, increased nest predation due to habitat loss and fragmentation, and the subsequent increase in the edge-to-area ratio of breeding habitat, is the most commonly cited reason for the decline of Neotropical migrant bird species (e.g. Askins et al. 1990, Askins 1995, Donovan et al. 1995, Robinson et al. 1995). Many species of birds breeding in small habitat fragments with high edge-to-area ratio experience higher rates of nest predation than those in larger forest tracts (e.g. Askins 1990, Askins 1995, Donovan et al. 1995, Robinson et al. 1995). In some forest stands, predation and nest parasitism are so high that these fragments function as population sinks rather than sources (Donovan et al. 1995).

The understanding of avian biodiversity in riparian habitat in eastern and northeastern North America has increased (e.g. Small and Hunter 1989, Gates and Giffen 1991, LaRue 1995, Whitaker and Montevecchi 1997), but avian biodiversity in buffer strips has not been as intensively studied. Only five studies to date have examined avian use of buffer strips (Johnson and Brown 1990, Triquet et al. 1990, Darveau et al. 1994, 1995, Whitaker 1997). Only the three most recent studies used replicated designs, and only Whitaker (1997) examined the relative importance of riparian and interior forest habitat for avian

richness and abundance. He found that avian richness and abundance was slightly higher in buffer strips compared to intact forest.

1.3 Indicators of Habitat Quality/Nesting Success

1.3.1 Density

Wildlife biologists often use animal density as an indicator of habitat quality (Van Horne 1983, Vickery et al. 1992). Most studies documenting avian habitat selection in riparian areas have used species richness and abundance as measures of habitat quality (e.g. McGarigal and McComb 1992, LaRue et al. 1995, Darveau et al. 1995, Whitaker and Montevecchi 1997), as have studies investigating avian use of buffer strips (Johnson and Brown 1990, Triquet et al. 1990, Darveau et al. 1995, Whitaker 1997). However, censusing avian richness and abundance may not provide reliable indicators of breeding success and population stability (Van Horne 1983). Vickery et al. (1992) found that density of some species of sparrows was negatively or not correlated with reproductive success.

These findings are especially important in the context of source-sink dynamics. Pulliam (1988) showed that reproductive surpluses from productive habitat can maintain populations in areas where reproduction is exceeded by mortality. Several recent studies have used nesting success to show that habitat

fragments function as population sinks for migrant song birds (Askins 1995, Robinson et al 1995, Donovan et al. 1995).

1.3.2 Nesting success

All of the above studies examining avian use of riparian habitat and buffer strips based their management recommendations on the assumption that avian richness and abundance in buffer strips are indicators of habitat quality. However, Maurer (1986) showed that nesting success, fledgling weight, and properties of nestling growth curves were better indicators of habitat quality than nesting density for five species of grassland birds. The most accurate way to measure breeding success is to monitor active nests for the numbers of fledged young (Martin and Geupel 1993). Although studies with natural nests are preferable when the abundance and density of nests allow for sufficient sample sizes to statistically analyze the question of interest (Martin and Geupel 1993), finding sufficient numbers of natural nests can be difficult in boreal systems (e.g. Darveau et al. 1997, I. Warkentin, pers. comm.).

1.3.3 Artificial nests

When natural nest studies are infeasible, artificial nests (i.e. small wicker baskets) are commonly used to assess the influence of fragmented landscapes on nest predation (see reviews by Paton 1994, Andrén 1995, Major and Kendall

1996). Artificial nests are especially useful for measuring nest predation; the most common cause of nest failure (Martin 1993). Wilson et al. (1998) found that predation patterns were similar between their artificial nest study and a study a real nests in the same area, but they recommended artificial nests be used in pilot studies. Furthermore, it is recognized that data from these studies can be used only as a relative index of predation pressure on natural nests (e.g. Rudnicky and Hunter 1993, Paton 1994, Haskell 1995a, Donovan et al. 1997). Artificial nests cannot be used to measure absolute predation due to biases such as lack of avian activity, scent in the vicinity of the nest, artificial nest placement, nest defense, and human presence.

Major and Kendal (1996) reviewed many of the biases and problems associated with artificial nests. Among the most important of these biases are the realism of the artificial nests, including nest and egg type, nest density, visibility, predator attractants, and exposure. For example, Martin (1987) found that increasing the realism of artificial nests, by covering them with moss, resulted in predation rates that more closely approximated those of real nests. Yahner and Voytko (1989) examined the importance of nest placement by comparing actual nest sites and random nest sites and found that predation rates were not significantly different. Perhaps most importantly Japanese Quail (*Coturnix japonica*) eggs, an egg commonly used in artificial nest studies, may not be appropriate to use in artificial nest studies, because their size may

exclude small mammalian predators from the experiment (e.g. Ropper 1992. Haskell 1995a).

Despite these potential biases. artificial nests have been used frequently to determine the effect of nest predation on avian nesting success in different habitats (Paton 1994. Andrén 1995. Major and Kendal 1996). Artificial nests aid in conducting experimental studies of nest predation, and have greatly increased understanding of the influences of edge effects and habitat fragmentation on avian nesting success.

1.4 Copper Lake Buffer Zone Study

The current management objective of the Newfoundland Forest Service's 20 Year Plan is to increase yearly timber harvests from 2.4 million m^3 to 5 million m^3 by the year 2035 while at the same time. attempting to protect forests for wildlife and recreation. Increases in timber production are to be achieved through increased silviculture (precommercial thinning and planting), forest protection (e.g. fire suppression. insect control), road building, and development of technology to utilize previously unmerchantable timber (Flight and Peters 1992). Much of the merchantable timber in the province is associated with riparian habitats resulting in a high probability for interactions between wildlife and forestry practices (Scruton et al. 1995). Current environmental protection guidelines for timber resource management in Newfoundland and Labrador

require the maintenance of a no-harvest, 20 m buffer strip along all water bodies that appear on a 1:50,000 scale topographic map (Scruton et al. 1995).

The Copper Lake Buffer Zone Study was initiated in 1993 by a consortium of public, private, and academic sectors to address the lack of information concerning the management of riparian habitat. A general description of the rationale, study area, methods and participating agencies for this multi-disciplinary research initiative is presented in Scruton et al. (1995). Various components of the project considered the influences of buffer strips on water quality, brook trout (*Salvelinus fontinalis*), terrestrial mammals, and forest bird assemblages. The research presented in this thesis investigated nest predation along the edges of riparian forest, buffer strips, and clear-cut edges in balsam fir (*Abies balsamea*) dominated forests in western Newfoundland.

1.5 Objectives

The current study assesses how well riparian buffer strips reduce the negative impacts of clear-cutting on breeding birds in the boreal forest and expands Whitaker's (1997) investigation of the composition and conservation of riparian bird assemblages in a balsam fir dominated ecosystem. Although avian richness and abundance are greater in buffer strips (Whitaker 1997), some research suggests that these indices may not be reliable indicators of nesting success (i.e. source/sink dynamics; Van Horne 1983, Pulliam 1988, Vickery et

al. 1992) and that forest birds may experience increased nest predation along both natural and artificial edges (Donovan et al. 1995).

The methodology is similar between the two experiments in this study and is presented in Chapter 2. An Introduction. Methods. Results and Discussion specific to each experiment is presented separately in Chapters 3 and 4. The objectives of experiment 1 (Chapter 3) were: 1) to assess the influence of buffer strips and habitat edges on nest predation. 2) to determine if buffer strip width influences nest predation. 3) to determine the importance of nest visibility and distance of the nest from the edge on nest predation, and 4) to identify nest predators. In experiment 2 (Chapter 4). my objectives were: 1) to compare predation levels on different sized quail eggs in artificial nests, and 2) to examine the importance of small mammals as nest predators in western Newfoundland.

Chapter 2. General Methods

2.1 Study Area

This study was conducted in western Newfoundland near the town of Corner Brook (48°57'N, 57°55' W). Study sites were located on 12 different ponds and lakes including Corner Brook Lake, Pike's Brook Pond, White Lady Lake/Watson's Pond, Whale Back Pond, Grindstone Pond, Beaver/Bar Pond, Sandy Pond, Meadows Pond, North Meadows Pond, Parson's Pond, Duck Pond, and Corner Brook Reservoir (Fig. 2.1, Tables 2.1 and 2.2). These water sheds are located in Newfoundland Forest Service Management Unit 15, which lies within the Corner Brook Subregion of the Western Newfoundland Ecoregion (Damman 1983).

Insular Newfoundland has a distinctive oceanic-forest biome (Robertson 1993), and the Corner Brook Subregion contains some of the most favorable sites for forest growth on the island. The region is characterized by forest, extensive clear-cuts, peatlands, and a rugged terrain with soils that are fertile relative to the rest of Newfoundland (Meades and Moores 1994). Forest fires are uncommon due to an average of 180 days/year of measurable precipitation (Damman 1983). The forest vegetation of the region is dominated by mature (60-80 year old) balsam fir forests. Black spruce (*Picea mariana*) is common but restricted to poorly drained sites (e.g. surronding peatlands and riparian areas)

and bedrock outcrops due to the low numbers of forest fires (Damman 1983). White spruce (*Picea glauca*), white birch (*Betula papyrifera*), yellow birch (*B. alleghaniensis*), red maple (*Acer rubrum*), northern wild raisin (*Viburnum cassinoides*), and mountain ash (*Sorbus americana*) are also present. The under-story of riparian ecosystems is composed primarily of blueberry (*Vaccinium* spp.), sheep laurel (*Kalmia angustafolia*), sweet gale (*Myrica gale*), and Labrador tea (*Ledum groenlandicum*; Ryan 1978). The under-story of interior forest is characterized by mosses, lichens, fallen trees, wild flowers (e.g. bunch berry *Cornus canadensis*), and forbs (e.g. yellow clintonia *Claytonia borealis*).

Vegetation along riparian edges is quite variable. Some areas have gradual vertical structuring to the forest canopy, while in other areas, the forest canopy occurs almost at the water's edge. Clear-cut edges are more uniform with an immediate transition between clear cuts and interior forest. Many run in relatively straight lines with sharp contrast between the logged and unlogged areas. However, on older clear-cuts, the definition of the edge is less distinct.

2.2 Regional Predators

Potential avian nest predators in western Newfoundland include Common Raven (*Corvus corax*), American Crow (*C. brachyrhynchos*), Blue Jay (*Cyanocitta cristata*), and Gray Jay (*Perisoreus canadensis*). None of these

birds were seen regularly on the study sites except Gray Jays (Whitaker and Montevecchi 1997, K. Lewis pers. obs.). Potential mammalian nest predators include black bear (*Ursus americanus*), red fox (*Vulpes vulpes*), American marten (*Martes americanus*), short-tailed weasel (*Mustela erminea*), mink (*M. vison*), red squirrel (*Tamiasciurus hudsonicus*), meadow vole (*Microtus pennsylvanicus*), and possibly masked shrew (*Sorex cineurus*; Scruton et al. 1995). Deer mouse (*Peromyscus maniculatus*) and eastern chipmunk (*Tamias striatus*) are rare but increasing in western Newfoundland (Tucker 1988). Compared to mainland North America, the potential predator assemblage is markedly reduced on insular Newfoundland. Common nest predators that are absent from the island include raccoon (*Procyon lotor*), skunk (*Mephitus mephitus*), gray squirrel (*Sciurus carolinensis*), wood rats (*Neotoma* spp.), and snakes.

2.3 Study design

2.2.1 Experimental design

The study design was similar between the two experiments. Experiment 1 was conducted in both 1996 and 1997, while experiment 2 was conducted in 1997. The general study design will be described here while specifics for each experiment will be given in Chapters 3 and 4. Artificial nest transects 200 m in length and parallel to the edge were established near lakes in three habitat

types: intact riparian forest controls (intact forest hereafter), clear-cut forest edges, and buffer strips (Fig. 2.2). Transects were placed along buffer strips with relatively constant width although width varied from 13-38 m among replicates (Table 2.2). All intact forest and buffer strip transects were parallel to lake edges. All clear-cut forest edge transects were placed to avoid roads, bogs, streams, insect-killed forest stands, and other forest openings. Buffer strip transects were placed as far from intact forest as possible. In 1996, in addition to studies with artificial nests, I attempted to study success of actual nests but found only nine. Hence, I abandoned this effort in 1997.

Shrub densities are similar between intact riparian forest and buffer strips in western Newfoundland. Vegetation along clear-cut forest edges had lower densities of black spruce but basal area was higher than on intact forest and buffer strip sites (Whitaker 1997). For more information concerning vegetation density, basal area, and species richness, see Whitaker (1997).

2.2.2 Artificial nest protocol

To measure predation pressures in different habitats, small wicker baskets (13 cm diameter x 5 cm depth) were used as artificial nests. Nests were filled with road side grasses and covered with moss from the study site to more closely approximate the appearance of real nests and real nest predation rates (1987). In 1997, smaller baskets were used due to availability (9 cm diameter x

3 cm depth). Nests were placed 5-15 m from the edge on buffer strip, clear-cut forest, and intact forest transects.

Nests were placed on the ground or in low branches of trees and shrubs. Ground nests were placed under a tree or fallen log in positions similar to White-throated Sparrow (*Zonotrichia albicolis*) nests (Harrison 1975). Suitable locations were common and additional foliage was rarely needed to increase nest concealment. Suitable locations for tree nests were more difficult to locate. Nests were placed in the fork of branches, under overhanging branches, or in the foliage of fallen trees. Nests were tied in place with black sewing thread in 1996 and black cable ties in 1997. Nests were placed between 1 and 2 m above ground in positions similar to Magnolia Warbler (*Dendroica magnollia*) and Blackpoll Warbler (*D. striata*) nests (Harrison 1975). Nest concealment was frequently increased on these nests by increasing the amount of foliage around the nest. White-throated Sparrow and Magnolia Warbler were the most common edge species in this area while Blackpoll Warbler is a forest generalist, i.e. a forest bird not clearly associated with riparian, interior, or clear-cut edge forest (Whitaker 1997). Nests were laid out during a period that coincided with the breeding seasons of these birds (Table 2.1: Whitaker 1997). Nests were inspected twice at 7 day intervals.

To minimize the chances of predators associating location markers with the nests (Yahner and Wright 1985), I placed flagging at 20 m intervals along

the riparian or forest edge approximately 10 m distance from the nests. When laying out nests, we wore rubber boots and attempted to minimize trails to the nests. To remove scent, nests were aired out for one day before setting them out in 1996, and for at least 5 days in 1997.

Many methods have been used to determine predators of artificial nests with varying degrees of success. I used artificial eggs molded from clay to identify nest predators. Using automatic cameras to identify predators is labor intensive, and they can rarely be purchased in sufficient quantity to identify predators at all study nests (e.g. Picman et al. 1993, Vander Haegan and DeGraaf 1996). Furthermore, predation at my sites was too variable to make this a reliable method. Major et al. (1994) found that adhesives, which can be used to obtain hair samples, were inappropriate for use in areas with frequent precipitation. Hair catchers, strips of sheet metal designed to catch hairs, have been found to attract predators (Yahner and Wright 1985). The most reliable means of predator identification, that can be applied to all nests, and has not been found to attract predators, is to use clay or plasticine "eggs" (hereafter referred to as clay eggs) to identify predator teeth and beak marks. This method has been used with a high degree of success by many researchers (e.g. Major et al. 1994, Haskell 1995b, Darveau et al. 1997, Donovan et al. 1997).

Japanese Quail (*Coturnix japonica*) eggs (JQE) were used in experiment 1 (Chapter 3) and both JQE and Chinese Painted Quail (*Xexcalfactoria*

chinensis) eggs (CQE) were used in experiment 2 (Chapter 4). Clay eggs were used In 1997. To identify nest predators, separate nests were baited and observed. I observed both red squirrels and Gray Jays at nests, and the clay eggs that they marked were immediately recovered, the marks observed, and compared to study eggs. A nest was considered preyed upon if either clay or quail eggs showed evidence of predation. Quail eggs in this study were obtained from the Quail Genetic Research Center at the University of British Columbia. All quail eggs were handled in 1996. In 1997, to remove any potential effects of human scent on eggs, eggs were washed and air dried and plastic gloves were used in all aspects of nest/egg handling and placement. No inter-annual comparisons were made on nest predation.

In 1997, distance from the nearest habitat edge (m), buffer strip width (m), and the visibility of the nest from above and from the sides was measured for each nest site. Visibility was measured by placing a 10 x 10 x 5 cm box with 25 equally spaced dots on top and 15 on each side on top of the nest. The number of dots visible from 1 m was used as an index of visibility (Major et al. 1994). Visibility from the side was calculated by averaging the number of visible dots from each side, observed at the same height as the nest and at a distance of 100 cm. Lower visibility indices indicate that nests are more higher concealed.

2.4 Statistics

Differences in predation on artificial nests were tested with logistic regression using SAS, PROC GENMOD (SAS Institute 1989-96). Logistic regression is a special form of the generalized linear model used for the analysis of binary or proportional response data with multiple explanatory variables (Agresti 1996). Logistic regression assumes a binomial random component (response variable) and a logit link function (McCullagh and Nelder 1989, but see Agresti 1996). Nests were either preyed on or not preyed on (i.e. binary), so a binomial distribution for the random component was appropriate. The link function specifies how the response variable is related to the explanatory variables in the linear predictor, i.e. the linear combination of the explanatory variables (Agresti 1996). The response variable in these experiments was the logit, natural log (p/(1-p)) of the number of predation events per transect.

Generalized linear models use deviance (or log-likelihood test), a generalized form of variance, for statistical inference. For logistic regression models, deviance is calculated for the intercept only model, $\mathbf{D_0}$. $\mathbf{D_0}$ is then subtracted from the deviance of the model $\mathbf{D_M}$. $\mathbf{D_0}$-$\mathbf{D_M}$ yields the "Model Chi-square" value or $\mathbf{G_M}$ (Hosmer and Lemeshow 1989, Menard 1995), which for many generalized linear models, has an approximately chi-squared distribution and is reported in an ANOVA style, analysis of deviance table (Agresti 1996). All results are reported as Type III analysis (analogous to adjusted sums of squares) unless otherwise noted in the text. Type I analysis (analogous to

sequential sums of squares) was used when the model for Type III analysis failed to converge.

Although nest density does not significantly influence predation in sub-boreal hardwood forests (Reitsma 1992) I investigated the independence of predation events on each transect. A Runs test ($\alpha = 0.1$) was used to determine if predation was spatially random (Zar 1984). In addition, I visually inspected all transects for signs of non-random predation in space and time, i.e predation on adjacent nests can occur in weeks 1 and 2 and therefore be independent. If predation within a transect was not randomly distributed and visual analysis indicated possible problems with independence, it was eliminated from the analyses. P-values for Runs tests were calculated on Minitab for Windows (1994).

All statistical tests were selected to individually test the objectives stated in each chapter and the appropriate models are presented in the statistical summary tables. The categorical explanatory variables used in this study were lake, experimental treatment, nest type, while buffer strip width, visibility (top and side), and distance of the nest from the edge are treated as continuous explanatory variables.

Chapter 3. Influences of Habitat, Nest Sites, and Predators on Nest Predation

3.1 Introduction

3.1.1 Habitat edges

Edge effects are the result of the interaction between two adjacent ecosystems, separated by an abrupt transition (Murcia 1995). While edges were originally believed to be beneficial for biodiversity and wildlife, evidence in the last two decades indicates that this phenomenon is not universal (Ratti and Reese 1988). Gates and Gysel (1978) proposed the ecological trap hypothesis, that birds are attracted to the vegetative diversity of edge habitats but experience greater nest predation due to higher predator activity. This hypothesis has been supported by many studies (e.g. Gibbs 1991, Fenske-Crawford and Niemi 1997). However, other studies have found predation risk to be lower at edges and higher in interior forest habitat (e.g. Small and Hunter 1988, Storch 1991), while other studies have found no evidence for edge effects (e.g. Yahner and Wright 1985, Ratti and Reese 1988, Picman et al. 1993, Rudnicky and Hunter 1993, Hanski et al. 1996). Andrén (1995) found that outside of the tropics, proximity to habitat edge and habitat patch size do not

influence nesting success in forested landscapes bordered by clear-cuts or young forests, suggesting that there may be few edge associated predators in these habitats.

Current thinking concerning edge effects and habitat fragmentation is that nesting success depends on edge type, fragment size, and predator assemblage (Andrén 1995, Robinson et al. 1995). Differences in the landscape mosaic and the behavioural ecology of different nest predators have been proposed as important mechanisms influencing predation in a fragmented landscape (Andrén 1995, 1997). Rather than documenting the existence or lack of edge effects, a shift to understanding the conditions that lead to edge effects should be pursued (Donovan et al. 1997).

3.1.2 Avian biodiversity in riparian habitat and buffer strips in the boreal forest

The unique habitat and vegetative structure of riparian edges often provides high quality breeding habitat for birds (e.g. Knopf et al. 1988, LaRue et al. 1995), yet few studies have specifically examined the value of riparian habitat for birds in the boreal forest. La Rue et al. (1995) found that median bird richness and density were significantly higher on riparian plots than interior forest and concluded that there was a positive edge effect. Whitaker and Montevecchi (1997) found no difference in total species richness and abundance

between riparian and interior forests, but found significantly higher avian diversity on clear-cut edges. However, species composition differed between forest types. For example, of the 34 bird species observed in their study in Newfoundland, the only common species that was significantly associated with riparian habitat was the Northern Waterthrush (*Seiurus noveboracensis*). Gray Jays and Dark-eyed Juncos (*Junco hyemalis*) were significantly more common on clear-cut edge transects than on intact forest transects.

Very few replicated, experimental studies have investigated avian biodiversity in buffer strips in eastern North America. Whitaker (1997) found that avian abundance was significantly higher in buffer strips compared to intact forest sites. Much of this difference was attributed to the juxtaposition of clear-cut habitat and clear-cut associated birds (e.g. White-throated Sparrows and Magnolia Warblers). Increasing buffer strip width had no effect on total avian richness or abundance, but abundance of interior forest specialist birds increased with buffer strip width. Darveau et al. (1995) found that 60 m wide buffer strips were wide enough to contain habitat used by interior species while 20 m wide buffer strips were not. 20 m buffer strips had higher initial populations after a cut, but had the fastest rate of species decline over three years. This initial "packing" and subsequent decline is likely due to the philopatric nature of migrant passerines and high rates of natural mortality. Larger buffer strips are more likely to support more avian species than narrow buffer strips in the long-

term due to greater habitat area and proportionally less habitat loss due to windfall (Darveau et al. 1994).

In addition to preserving habitat, buffer strips may have important roles in avian dispersal and habitat conservation. Buffer strips act as dispersal corridors for juvenile migrants and movement corridors for forest birds (Machtans et al. 1996). Abundances of five species of Neotropical migrants were higher in forest fragments connected by buffer strips than in isolated fragments (Schmiegelow et al. 1997).

3.1.3 Artificial nests studies in coniferous forests

Andrén (1995) reviewed studies that examined the effects of edge and patch size on nesting success and nest predation. He found that edge-related increases in nest predation were commonly found in forests fragmented by agriculture, but were rarely found in forests fragmented by clear-cuts. This finding of differential nest predation along agricultural and clear-cut edges has been shown in subsequent studies (Marini et al. 1995, Bayne and Hobson 1997, Donovan et al. 1997).

Few researchers have studied the influences that lake edges and logging practices have on nesting success in boreal forests (see Paton 1994, Andrén 1995, Major and Kendall 1996). Pöysä et al. (1997) found that predation rates on nest boxes for Common Goldeneye (*Bucephala clangula*) were not affected

by distance to the shore, and Bollinger and Peak (1995) found that predation rates were similar at forest-lake and forest-field edges.

The effects of buffer strips on nest predation have only recently been explored. In Maine, Vander Haegan and DeGraaf (1996) found that although differences in nest predation were not great, nest predation was significantly lower on intact forest sites compared to 20-40 m buffer strips and 60-80 m buffer strips. Red squirrels and Blue Jays accounted for more than 50 % of the identified predations on a subset of these nests. In the boreal forest of Quebec, Darveau et al. (1997) found that predation risk was higher in 40-60 m buffer strips than 20 m buffer strips and intact forest sites. Red squirrels preyed on 36 % of the nests and were the dominant predator; birds accounted for 13 % of the predations.

3.1.4 Objectives

My research objectives were to determine: 1) if predation was higher on buffer strips than intact riparian forest, 2) if predation differed between riparian and clear-cut forest edges, 3) if predation varies with buffer strip width, 4) if nest visibility and distance of the nest from the forest edge influenced nest predation on different treatments, and 5) the local predator community and their nest predation patterns.

3.2 Methods

In 1996, I established five study blocks and added two in 1997, to improve statistical power. More sites could not be added due to the limited number of sites that fit my study design. Lake size was usually small (< 44 ha) although two lakes were large (125 and 561 ha; Table 2.2). Buffer strips were narrow (13-38 m), and sites had been logged between 1989 and 1991(Table 2.2). In 1996, 10 baskets were placed at 20 m intervals along a 200 m transect (n = 150), while 20 were set out on 200 m transects in 1997 (n = 420). Increases in nest density were necessary to improve statistical power due to the limited availability of study sites. Two JQE were placed in each nest in 1996, and in 1997, two JQE and two clay eggs, one attached with monofilament were placed in each nest. Nests were generally placed in an alternating pattern but this pattern was broken according to availability of tree nest sites. Nests were set out from June 16-20 and June 10-16 and checked from June 30-July 4 and June 24-30 in 1996 and 1997 respectively (Table 2.1).

Variables for the logistic regression models were chosen to fit the objectives previously described and calculated using PROC GENMOD (SAS Institute Inc., 1996). Statistical analyzes were performed on cumulative predation events. Experimental treatments were divided into edge treatments (Intact Forest:Clear-cut) and habitat treatments (Buffer Strip:Intact Forest) to determine the influences of logging practices on avian nesting success. Nest

type (ground or tree, k = 2) and the interactions between treatments (k = 3)and nest types were included in the models to determine if these variables influenced predation. Lake (1996: k = 5, 1997: k = 7) and the interactions between lakes and treatments were included to determine if nest predation among replicates varied with study sites. The influence of buffer width on nest predation was tested with no other variables.

Nest predation was not randomly distributed on two transects (Runs P > 0.1) in 1997 and a random distribution was questionable on four transects based on visual analysis. However, when these data were eliminated from the analysis, the significance of the terms in the logistic regression models did not change except for nest type in the 1997 edge comparison. Results from this test do not include those transects.

A general linear model analogous to multiple analysis of variance (MANOVA) was used to test for the influence of distance of the nest from the edge on visibility and the influence of visibility on different nest types using PROC GLM (SAS Institute 1989-1994). Logistic regression was used to determine the influence of distance from the edge and visibility on nest predation. With PROC GENMOD (SAS Institute 1989-9994), I used a log-linear model, a generalized linear model with a Poisson error distribution and a log link, to test for differences in number of predations by red squirrels and Gray

Jays in different forest treatments and nest types (Sokal and Rohlf 1995, Agresti 1996).

3.3 Results

3.3.1 Edge and habitat comparisons

Nest predation was highest on intact forest sites over both years. Predation was lowest on buffer strips in 1996 and lowest on clear-cut edges in 1997 (Table 3.1). When buffer strips and intact forest sites were compared, predation was significantly influenced by the interaction between lake and treatment in 1996 and 1997, and tree nests experienced significantly higher predation than ground nests in 1997 (Fig. 3.1, Tables 3.1, 3.2). Predation was highly variable among lakes in both years (Tables 3.3, 3.4). When clear-cut forest edges and intact forest were compared, predation was significantly influenced by lake in 1996 (Tables 3.2, 3.3), and by the interaction between lake and treatment in 1997 (Tables 3.2, 3.4). Overall, predation levels among lakes ranged from 22 - 79 %, and when sub-divided by treatments and nest type, predation levels ranged from 0 -100 % (Tables 3.3, 3.4).

3.3.2 Buffer strip width

I examined the effect of buffer strip width on predation by pooling the results of 1996 and 1997. Buffer strip width had a significant and positive influence on predation (Table 3.2, Fig 3.2).

3.3.3 Distance of the nest from the edge and nest visibility

Distance of the nest from the edge did not influence top or side visibility on any treatment (P's > 0.05, r^2's < 0.03). Ground nests were more concealed from the side than tree nests on all treatments (Table 3.5). Visibility from above was only significant on clear-cut forest edges ($F = 77.8$, $df = 1$, $P < 0.0001$).

There was an overall trend for predation to increase as nest visibility from the side increased (Fig. 3.3), but this trend was significant only on intact forest edges (Table 3.6). Distance from the edge positively influenced predation on buffer strips but negatively on intact forest edges (Fig 3.4, 3.5).

3.3.4 Predators of artificial nests

I was able to determine whether a predator was a bird or a mammal for 42 % (n = 33) of the ground nests and 48 % (n = 49) of the tree nests (Table 3.7). These low percentages were due to both types of quail eggs being consumed without any marks being left in the clay eggs, or all the nest contents or rarely the entire nest disappearing. Mammals preyed on 39 % of the ground nests and 26 % of the tree nests based on shell fragments remaining at the nest (Table 3.7). The predators that I was able to identify at the species level were red squirrels and Gray Jays. Red squirrels preyed on 6 ground nests (12 %) and 10

of the tree nests (10 %). Gray Jays preyed on 3 of the ground nests (4 %) and 22 of the tree nests (22 %; Table 3.7). Red squirrels and Gray Jays preyed on tree nests significantly more than ground nests ($G = 11.8$, $df = 1$, $P = 0.0006$). Differences in species specific predation on nest types were large but not significant (Table 3.7, $G = 3.6$, $df = 1$, $P = 0.0564$). Predation by red squirrels and Gray Jays was similar on buffer strips, intact forest sites, and clear cut-edges (Table 3.7, $G = 1.7$, $df = 2$, $P = 0.4308$).

3.4 Discussion

3.4.1 Influences of edge and habitat

The main objective of this study was to determine if buffer strips were sites of high nest predation and if nest predation differed between edge types. Predation does not increase in buffer strips, rather, these results indicate that nest predation is not influenced by the experimental treatments but is influenced by the specific location. Predation is site-specific in western Newfoundland, perhaps due to the patchy distribution of predators and their behavioural ecology differentially affecting nest predation (Andrén 1995, Lima and Zollner 1996). The large differences in nest predation among lakes sites in this study may also indicate that an unaccounted for, intermediate landscape variable is influencing nest predation. Other studies have also found a great deal of inter-lake variability in predation levels (Bollinger and Peak 1995, Pöysä et al. 1997).

While other studies on nest predation in buffer strips (Vander Haegan and DeGraaf 1997, Darveau et al. 1997) have not investigated the influences of clear-cut forest edges, differences in edge did not influence absolute predation but may influence behaviour (See 3.4.3).

3.4.2 Influences of buffer width

Although predation is highly site-specific, resulting in some narrow buffer strips with high nest predation, there is a general trend for buffer strip width to influence nest predation. Predation may tend to increase in wider buffer strips because they provide more habitat for predators. For example, European red squirrels (*Scurius vulgaris*) are more likely to be found in larger woodlot fragments (Verboom and van Apeldoorn (1990).

Lower predation in narrow buffer strips, does not necessarily indicate that narrow buffer strips benefit avian populations more than wider ones for several reasons. First, assuming that wider buffer strips have more avian habitat and more potential nest sites, then bird nests in a 50 m wide buffer strip may incur higher levels of predation, but produce more fledglings than in a 20 m wide buffer strip. Second, numbers of interior forest species increased with buffer strip width (Whitaker 1997); these interior forest species are currently experiencing population declines in North America (Askins 1995, Robinson et al. 1995). Third, windfall loses will be proportionally higher in narrower buffer

strips, reducing habitat value in the long term (Darveau et al. 1994). Windfall losses are likely to be aspect dependent but in some cases, 20 m wide buffer strips were reduced to 10 m due to windfall. Finally, buffer strips may act as corridors for avian dispersal and movement between habitat fragments (Haas 1995, Dunning et al. 1995, Machtans et al. 1996, Schmiegelow et al. 1997), indicating the importance of maintaining the integrity of buffer strips.

3.4.3 Distance of the nest from the edge and nest visibility

Although vertical structure of vegetation often increases at riparian habitat edges (LaRue et al. 1995 and references therein), distance from the edge had very little influence on nest visibility possibly due to variability in vegetative cover at riparian edges. While clear-cut edges were relatively homogeneous in their lack of vertical vegetative structure, shrub densities at riparian edges differed greatly.

Ground nests were more concealed than tree nests on all treatments due to high levels of ground cover and fallen logs. Greater visibility of ground nests may explain lower predation levels relative to tree nests (Martin 1993). The greater visibility from the top tree nests compared to ground nests on clear-cut forest edges is probably due to differences in forest composition between clear-cut forest and riparian forest edges. Interior forest adjacent to the clear-cut

forest edge usually had little shrub growth and few branches below 2 m, the height where tree nests were placed resulting in greater nest exposure.

If vegetation structure increases at edges, then nests should be more concealed near the edges. Since this was not shown in this study, it is surprising that predation is influenced by distance from the edge. While this difference occurred over small distances (<20 m), it may indicate that predators prefer moving along edges and prefer clear-cut edges to riparian edges. I do not know why side visibility influenced predation on intact forest sites but did not on buffer strips.

3.4.4 Predators

This study implicated Gray Jays and red squirrels as the major nest predators in western Newfoundland. Gray Jay predation was accurately determined. I observed Gray Jays trying unsuccessfully to pull the tethers off the clay eggs and they always left very characteristic beak marks in the clay. The results for red squirrels nest predation are less reliable because this species was more difficult to observe. A possible reason for high predation rates on some transects and low predator identification rate is that red squirrels learned to avoid clay eggs. Initially, red squirrels preyed on several nests on a transect leaving teeth marks in the clay eggs, but subsequently, many nests were found with the quail eggs gone and the clay eggs untouched. It is likely

that red squirrels preyed on eggs in these nests. If this is the case, the results of this study may seriously underestimate nest predation by red squirrels in Newfoundland.

These findings are consistent with other studies in coniferous forests in which red squirrels have been identified as a major nest predators (Vander Haegan and DeGraaf 1996, Bayne and Hobson 1997, Darveau et al. 1997). Other species of squirrel have also been implicated as major nest predators (O'Reilly and Hannon 1989).

Nest predation by red squirrels is of special concern in Newfoundland where the species was introduced in 1963 (Tucker 1988, Montevecchi et al. submitted). The red squirrel is abundant in Newfoundland but appears to be most abundant in black spruce forests (Reynolds 1997, Montevecchi et al. submitted, S. Wren and J. Gosse pers. comm.). Thus, it is likely that nest predation will be higher on the east coast of Newfoundland (black spruce dominated) than on the west coast (balsam fir dominated). However, given the ubiquity of nest predation by red squirrels, this increase in abundance is not likely to change nest predation patterns between riparian and non-riparian sites. Furthermore, in evolutionary time, the birds of insular Newfoundland have not been exposed to any arboreal, mammalian nest predators except the rare American marten. The long-term implications of the introduction of red squirrels to avian populations on insular Newfoundland is unknown. However, given their

high densities and potential for finding both ground and arboreal nests, the red squirrel could be detrimental for many avian species that breed in Newfoundland (Montevecchi et al. submitted) and may have implications for other taxa (Moessler et al. submitted).

It is unlikely that small, mammalian predators other than red squirrels influence nest predation in insular Newfoundland. Meadow vole are unlikely to be a major nest predator in this study because they prefer open, unforested areas (Nichols 1995, Thompson and Curran 1995). Masked shrews and eastern chipmunks were introduced to Newfoundland in 1958 and 1962 respectively, and deer mice were first found on the island in 1968 (Tucker 1988). Masked shrews are found in nearly all the habitats on insular Newfoundland, but populations are not large (Nichols 1995). Various species of shrew are known to visit artificial nests (Nour et al. 1993, Darveau et al. 1997), but there is no evidence that they are nest predators. Deer mouse and eastern chipmunk populations are very low and largely confined to parts of western Newfoundland, although they are slowly increasing (J. Brazil pers. comm.). The effect that increasing populations of these small mammals will have on nest predation is also unknown. Eastern chipmunks may compete with red squirrels for other resources, but there could be a cumulative effect on nest predation.

3.4.5 Other buffer strip studies

Comparisons between this study and the findings of Vander Haegan and DeGraaf (1996) and Darveau et al. (1997) are equivocal. Vander Haegan and DeGraaf (1996) found that predation rates were significantly higher in buffer strips (23 %) than intact forest (15 %) and that predation was similar between mainstream and tributary buffer strips. Darveau et al. (1997) found that predation was highest on 40-60 m wide buffer strips and lower on 20 m wide buffer strips and intact forest. In contrast, my study found that predation was often highest in intact forest and that predation is likely to be site-specific. These differing results indicate that predation may be influenced by predator density and behaviour along edges. In areas where edge predators are common, the double edge of a narrow buffer strip may compound predation rates. In areas where predators are territorial and forest specialists, elimination of forest should decrease or maintain predation rates.

The primary conclusion that can be made from my study of real nests is that documenting nesting success on a large scale, as has been done at mainland sites (Donovan et al. 1995, Robinson et al. 1995), will be extremely difficult in Newfoundland. Although this study was conducted in a landscape that was not logged specifically for an experimental study, other factors that will impede attempts to find large samples of nests are low nesting densities, short nesting seasons, dense vegetation, rough terrain, windfall, and biting black flies that obscure vision. Other studies in the boreal forest have found it difficult to

find real nests. For example, Darveau et al. (1997) gathered information on only 24 nests in a large, four year study. Use of small radar tags and portable transmitter-receivers may help in nest searching and location (Roland et al. 1996). Clearly, a more concentrated research effort must be made to determine the influences of buffer strips on nesting success in the boreal forest, although this may not be logistically feasible in Newfoundland.

3.4.6 Uniqueness of Newfoundland boreal forests

The forests of Insular Newfoundland have certain unique characteristics that may change the ways in which habitat fragmentation influences nest failure of both artificial and real nests. Mammalian species diversity and population densities are very low on the island (Nichols 1995). Predators that play major roles in nest failure elsewhere, such as raccoons, skunks and snakes, are not found in Newfoundland (Scruton et al. 1995) so the concept of edge effects, especially the ecological trap hypothesis (Gates and Gysel 1978), may not be relevant or applicable in Newfoundland forests. In contrast, Donovan et al. (1997) conducted a regional study in the mid-western United States, an area with many edge associated predators, and found that nest predation on edges was greater than in core habitat. Also, Newfoundland has few Brown-headed Cowbirds (*Molothrus ater*), nest parasites that are often associated with habitat edges, and have been implicated in population declines of Neotropical migrants

(Robinson et al. 1995). Finally, anthropogenic forest fragmentation in Newfoundland is almost exclusively due to clear-cutting. Bayne and Hobson (1997) found that forests fragmented by agriculture had higher predation levels than those fragmented by clear-cuts. With few edge predators or cowbirds, and very little forest fragmented by agriculture, Newfoundland may represent a best case scenario for edge nesting species in North America. However, the predation pressures on interior forest birds in Newfoundland remains to be studied.

Chapter 4. Predation on Different-sized Quail Eggs

4.1 Introduction

Artificial nest studies that examine the influence of habitat alteration on nest predation commonly use Japanese Quail eggs (JQE; e.g. Gottfried and Thompson 1978, Wilcove 1985, Small and Hunter 1988, Reitsma et al. 1990, Rudnicky and Hunter 1993, Seitz and Zegers 1993, Bayne et al. 1997). However, the influence of egg type and size on the results of artificial nest studies has only recently been experimentally tested (Nour et al. 1993, Haskell 1995a, 1995b, Bayne et al. 1997, DeGraaf and Maier 1996, Craig 1998).

JQE are substantially larger, have thicker egg shells, and tend to be more spherical than the eggs of Neotropical migrants and other passerines of the boreal forest. Small mammals may not have gapes wide enough to break JQE shells (Roper 1992, Haskell 1995b, DeGraaf and Maier 1996, but see Craig 1998). However, many small mammals such as *Peromyscus* and *Microtus* spp. prey on the eggs of many ground- and tree-nesting species (Maxson and Oring 1978, Guillory 1987, Bureš 1987). The potential inability of JQE to account for predation by small mammals suggests that artificial nest studies with JQE may produce biased estimates of relative predation rates.

In addition to underestimating relative predation by excluding small mammals from nest predation studies, using JQE in artificial nest studies may

result in a more important bias when nest predator assemblages differ between experimental treatments and locations. Using modeling clay "eggs", Haskell (1995a) found that excluding predation by small-mouthed predators from nest predation studies can produce highly misleading results. He found a positive relationship between increasing forest-fragment size and predation by small mammals and a negative relationship for predation by large mammals. Nour et al. (1993) used plasticine eggs and also found that nest predation by small mammals increased with fragment size, compensating for a decrease in nest predation by birds in large fragments. Had Nour et al. (1993) and Haskell (1995a) exclusively used JQE, which may not detect small mammal predation, they would have erroneously concluded that fragment size influences predation rates. Fragment size did not influence overall predation in these studies but did influence the types of predators. Based on these studies, it is clear that experiments investigating nest predation should use eggs that approximate the actual size of eggs of birds nesting in the area, especially when predator types and densities differ across landscape mosaics (Bayne and Hobson 1998). Only 35 % of the studies reviewed by Major and Kendal (1996) used eggs that approximated the egg size of the potential prey species. Chinese Painted Quail and Zebra Finch (*Taenopygia guttata*) eggs are much smaller than JQE and more closely approximate the size of large and small passerine eggs

respectively (Haskell 1995b). These eggs may be more appropriate eggs to use in artificial nest studies.

While clay eggs have been used in artificial nest studies (Nour et al. 1993, Haskell 1995a), Bayne et al. (1997) found that plasticine eggs suffered higher predation than JQE and that predation differed between habitats depending on type of egg used. Although clay eggs are useful (i.e. inexpensive and informative), it needs to be determined if and how they influence predation before they are extensively used in place of real eggs in artificial nest experiments.

In the boreal forest, small mammals have accounted for 7-23 % of nest predation (Bayne and Hobson 1997, Darveau et al. 1997, Hannon and Cotterill 1998). On insular Newfoundland, small mammals may play a proportionally greater role due to the absence of snakes, skunks, and racoons, and relatively low densities of other mammals. Despite low mammalian densities on insular Newfoundland (Nichols 1995), it needs to be determined if small mammals are important predators of passerine nests.

The purpose of this study was to determine 1) if Chinese Painted Quail eggs, which are smaller than JQE, suffer different levels of predation in different habitats than JQE in artificial nest experiments in western Newfoundland, and 2) if small mammals are important nest predators in western Newfoundland. If small mammals that cannot consume JQE are important nest predators, I expect

to detect higher predation on CQE than JQE. i.e. are CQE more appropriate than JQE for use in artificial nest studies in Newfoundland?

4.2 Methods

4.2.1 Study design and experimental protocol

The methods in this experiment were very similar those in experiment 1. Lakes were small (7-25 ha), buffer strip width was narrow (18-33 m), and sites were logged between 1988 and 1991. In 1997, I established five transects along intact riparian forest edges and four along buffer strips of varying width (Table 2.1, Table 2.2). Transects were 200 m in length; intact forest transects were placed in plots which were at least 150 m wide, and buffer strip transects were placed as far from intact forest as possible.

Twenty artificial nests (wicker baskets 9 cm diameter x 4 cm deep), lined with grass and covered with moss, were placed at approximately 10 m intervals along each 200 m transect. Nests were placed on the ground only (n=180). A single JQE or CQE was placed in each nest along with a clay egg tethered to the nest. Ten nests containing each egg type were placed in an alternating pattern along each transect. Nests were set out from June 17-21 and checked from July 1-5 1997 (Table 2.1). Subsets of 149 JQE and 80 CQE were measured for length and width before the field season to the nearest 0.1 mm using digital calipers.

4.2.2 Statistics

Egg volume was calculated using the formula for the volume of an ellipsoid. $V = \pi/6(LW^2)$ where V is the volume. L is the egg length, and W is the egg width (Preston 1974). This formula has been used to estimate Thick-billed Murre (*Uria lomvia*) egg volume. eggs that greatly differ from ellipsoid with 95 % accuracy (Birkhead and Nettleship 1981). Comparisons between egg width and volume were made using a one tailed t-test for two means without assuming equal variance (Sokal and Rohlf 1995. Minitab Inc.1994).

Logistic regression was used to determine if nest predation was influenced by lake site (n = 5). buffer strip v. intact forest (n = 2). and egg type (n = 2) using PROC GENMOD (SAS Institute. Inc. 1996). I tested to see if predation on different-sized eggs varied between habitat treatments and if there was an interaction between habitat treatments and egg size. Predation was spatially random (Runs P > 0.1) on all transects. except one where predation was temporally independent.

4.3 Results

JQE were 4 mm wider than CQE (JQE = 23.7 +/- 0.6 mm, CQE = 19.7 +/- 0.6 mm). JQE were nearly twice the volume of CQE (JQE = 9.1 +/- 0.7 ml, CQE = 5.09 +/- 0.5 ml). The difference between eggs for both width and volume was significant (width, t = 47.2, df = 228, P < 0.0001; volume, t = 53.8, df = 228. P <

0.0001). There was no difference in predation due to buffer strip or intact forest sites ($G = 2.371$, $df = 1$, $P = 0.12$), and there was no difference in predation due to egg type ($G = 1.360$, $df = 1$, $P = 0.24$; Table 4.1).

Of 123 predation events, 32 % were identified using clay eggs or by examination of the condition of the nest/eggs. 11 % were identified as red squirrels and 21 % were unidentified mammals. Based on clay eggs, there were no avian predators on these ground nests.

4.4 Discussion

4.4.1 Egg size and predators

This is the first experimental test, at a landscape scale, to assess how different sized quail eggs influence predation in an artificial nest experiment. I attempted to test Haskell's (1995b) and Ropper's (1992) observations that JQE bias the results of artificial nest studies by excluding small mammalian predators. Although Bayne et al. (1997) studied how different sized-eggs affect predation, they compared JQE to plasticine eggs. DeGraaf and Maier (1996) showed how egg size affects predation by a single species.

I found that the different-sized JQE and CQE had little influence on predation, indicating that despite being much smaller, CQE did not improve the sensitivity of artificial nest experiments in Newfoundland. If mammals smaller than red squirrels are important nest predators, and if they can consume CQE,

predation on smaller-sized eggs should have increased. There was no evidence of predation by small mammals based on the clay eggs in either experiment 1 or 2. Although I may not have detected small mammal predation through the use of clay eggs, it is unlikely that small mammals other than red squirrels are important nest predators for a number of reasons.

The two small mammals that are abundant in western Newfoundland are masked shrew and meadow vole (Tucker 1988). Even in peak years, small mammal densities in western Newfoundland are relatively low (Nichols 1995). Nour et al. (1993) and Darveau et al. (1997) found shrew-like teeth marks in plasticine eggs, though there is no direct evidence that shrews (*Sorex* spp.) prey on bird's eggs. Thompson and Curran (1995) reported that meadow voles were not found in second-growth stands and therefore, would be an unlikely nest predator on our study sites.

The role of egg size in nest predation studies requires more investigation. Egg widths of a number of eastern North American passerine species common in this area average from 12.3 -15.5 mm for warblers, 15.5 mm for White-throated Sparrow, 16.8 mm for Hermit Thrush, 18.3 mm for Pine Grosbeak, 18. 6 mm for Rusty Blackbird, and 20.0 mm for American Robin (Harrison 1975). CQE width falls near the high end of this range making them an useful substitute for studies of larger passerines such as American Robin. Whether CQE are

small enough to assess predation by potential predators like eastern chipmunks, deer mice, meadow voles, and masked shrews remains to be determined.

Haskell (1995b) assumed that egg width is the factor limiting a predator's ability to break an egg shell. However, small predators may try to break open ellipsoidal eggs at the narrower pole (Craig 1998). I observed that Gray Jays had difficulty picking up JQE and carried off eggs with the narrower pole in their bills, and some eggs were eaten from the narrower pole. Crows exhibited similar behavior with extremely large eggs (Montevecchi 1976). JQE, which are almost twice as voluminous as CQE, may be too large for small mammals to manipulate, i.e. brace in a position where they can effectively bite the narrow pole of the egg. While we did not measure the width of the narrow pole, egg volume gives a rough estimate of relative egg size that a predator can handle and consume. Based on these observations, a predator may be able to consume an egg with a width wider than its gape (Craig 1998). Simple behavioural observations of small mammals may identify the limiting factors in egg consumption and indicate the most appropriate egg size to use in artificial nest experiments (Haskell 1995b, DeGraaf and Maier 1996, Craig 1998).

4.4.2 Methodological considerations

While an egg that approximates the egg size of the target species is desirable, they are not always available in the required quantities (Craig 1998).

I have shown that CQE do not affect predation levels in western Newfoundland, but CQE may still be too large for some small mammals to consume. Future experiments should incorporate several natural eggs of different sizes. For example, both quail eggs used in this experiment and Zebra Finch eggs could be incorporated into this experimental design. However, Zebra Finch eggs may be inappropriate if they are smaller than the eggs of target species (Craig 1998).

Knowledge of predator abundance, distribution, and population dynamics is also useful in artificial nest experiments. Bayne et al. (1997) found that red squirrels were more abundant and predation was higher in coniferous than in deciduous forests. The cyclic nature of some small mammal populations and species habitat preference may influence the results of nest predation studies (Darveau et al. 1997). A variable that may alter the results of this study over time is the increasing abundance of introduced eastern chipmunks and deer mice on insular Newfoundland (Tucker 1988, Montevecchi et al. submitted, J. Brazil pers. comm.). While the current geographic ranges of these species are mostly limited to western Newfoundland, they are expanding. If eastern chipmunks and deer mice continue to disperse across the island, nest predation rates will likely increase, and JQE may not be an appropriate egg to use in artificial nest studies in Newfoundland. Fluctuations in small mammal densities and changes in distribution can influence predation rates at the landscape level

and could bias the management recommendations based on short-term artificial nest studies.

Finally, researchers interested in performing meta-analyses on edge effects or habitat fragmentation, and in making management recommendations based on artificial nest data, should critically review past artificial nest studies to determine if egg size potentially biased the results of these studies. Egg size is not the only variable that may influence predation between habitat types but its potential to bias artificial nest studies by discriminating against certain predators requires that researchers attempt to control for this variable in their research designs.

Chapter 5. Concluding Discussion and Summary

5.1 Nest Predation in Fragmented Forests

Many studies assume that predators forage along habitat edges, and have searched for an edge effect in disturbed habitat (e.g. Yahner and Wright 1985, Ratti and Reese 1988, Small and Hunter 1988, Gibbs 1991, Storch 1991, Picman et al. 1993, Rudnicky and Hunter 1993, Hanski et al. 1996, Fenske-Crawford and Niemi 1997). However, no studies have found an edge effect on nest predation in coniferous forests fragmented by clear-cuts (Andrén 1995), although an edge effect was found in a forest fragmented by prescribed fire (Niemuth and Boyce 1997). Bayne and Hobson (1997) found predation levels were similar between areas logged (25 % of total area) and contiguous forest landscapes. My findings that nest predation does not increase due to logging in fragmented, coniferous forests, are consistent with these results.

5.2 Recommendations for Buffer Strip Width

This study found that predation does not increase in buffer strips relative to intact forest, indicating that birds not only use buffer strips (Whitaker 1997), they also successfully reproduce in them. The findings of this study were in agreement with Darveau et al. (1997), who found that predation increases with buffer strips width. As discussed earlier, this does not indicate that narrow buffer

strips are better for birds. Avian abundance is higher in wider buffer strips compared to narrow ones (Whitaker 1997) which may result in higher total reproductive output. Windfall also greatly reduces the effectiveness of narrow buffer strips (Darveau et al. 1994). Whitaker (1997) concluded that leaving buffer strips 20-50 m wide provided habitat for birds from a number of habitat guilds. However, buffer strips did not adequately conserve interior forest species, and narrower buffer strips had lower numbers of interior forest birds. Vander Haegan and DeGraaf (1996) recommend that buffer strips be at least 150 m wide to preserve interior forest birds. This recommendation is impractical in Newfoundland where lakes, ponds, streams and rivers are extremely abundant. An alternative suggestion is to maintain some large, relatively symmetric tracts of forest to conserve interior forest species (Whitaker 1997).

5.3 Scope and Limitations

The findings of this study are applicable to lake shore and clear-cut edges of balsam fir forests in western Newfoundland and other areas of the boreal forest with similar predator assemblages. No attempt was made to investigate nest predation in interior forest habitat or clear-cuts. Although predator assemblages on insular Newfoundland are much more limited than those on mainland North America (Scruton et al. 1995), these results were similar to other

studies of nest predation in boreal and coniferous forests (e.g. Andrén 1995, Darveau et al. 1997, Bayne and Hobson 1997).

Although artificial nests are only a surrogate model of actual nest predation, they are the best available means to assess the influences of habitat alteration on nest predation in the boreal forest. The sophistication of artificial nest studies continues to increase and provide valuable information on how anthropogenic induced habitat alteration influences nest predation.

5.4 Future Research

The results of this study and others would be significantly improved when integrated with information on predator densities (Bayne and Hobson 1997), predator habitat preferences (Andrén 1995), and predator foraging behaviour (Lima and Zollner 1996). Winter tracking, combined with small mammal trapping in the summer may reveal local predator assemblages, home ranges, and habitat preferences. Using video cameras or other means of observation near real and artificial nests could show how predators search for nests and consume eggs (e.g Craig 1998). Future studies should also attempt to maximize the number of study sites, replicate actual nest densities, and find a more comprehensive means of predator identification.

The decline of interior forest birds across eastern North America is of increasing concern, and comparisons of interior forest with clear-cut edges,

clear-cuts, riparian edges, and fragments of varying size will aid in making better informed management decisions. Vander Haegan and DeGraaf (1996) and Darveau et al. (1997) examined nest predation in buffer strips along rivers, while I examined nest predation along lake shores. Rivers in Newfoundland vary greatly in size, and predation on forest-river edges may differ from forest-lake edges. Comparisons of buffer strips along lakes and rivers should be made to determine if nest predation and predator assemblages and behaviour are similar near lakes and rivers. Finally, precautionary principles make it clear that preservation of both riparian and interior forest habitat has to be a management and conservation priority.

5.5 Summary

Predation was significantly influenced by study site, buffer strip width, and visibility. Tree nests were generally more vulnerable than ground nests, and Gray Jays and red squirrels were the only nest predators identified. Real nests were very difficult to find and may seriously hinder future attempts to study the effects of landscape alteration on avian nesting success in boreal forests. Japanese Quail eggs, which have been used in many studies to assess the influence of habitat change on nesting success, are presently appropriate for use in Newfoundland. While small mammals do not seem to be important nest predators, increasing populations of some introduced small mammals, especially

red squirrels. may have serious long-term consequences on avian nesting success in Newfoundland.

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Table 2.1. Study sites and dates for different experiments. Dates for 1997 are in parentheses. Month is only given in parentheses if months differ in 1996 and 1997. Lake abbreviations are used in Figure 3.2, and Tables 2.2, 3.3, and 3.4. Numbers are used in Fig. 2.1.

No.	Year	Lake	Experiment	Nests Out	Nests Checked
1	1996(97)	Corner Brook Lake (CBL)	1	JUN 16 (10)	JUN 30 (24)
2	1996(97)	Pike's Brook Pond (PBP)	1	JUN 17 (11)	JUL 1 (JUN 25)
3	1996(97)	White Lady Lake (WLL)	1	JUN 18 (12)	JUL 2 (JUN 26)
4	1997	Whale Back Pond (WBP)	1	JUN 13	JUN 27
5	1997	Grindstone Pond (GSP)	1	JUN 14	JUN 28
6	1996(97)	Beaver/Bar Pond (BBP)	1	JUN 19 (15)	JUL 3 (JUN 29)
7	1996(97)	Sandy Pond (SAP)	1	JUN 20 (16)	JUL 4 (JUN 30)
8	1997	Meadow's Pond (MP)	2	JUN 17	JUL 1
9	1997	Duck Pond (DP)	2	JUN 18	JUL 2
10	1997	Parson's Pond (PP)	2	JUN 19	JUL 3
11	1997	Norman's Pond (NP)	2	JUN 20	JUL 4
12	1997	Corner Brook Reservoir (CBR)	2	JUN 21	JUL 5

Table 2.2. Study site location, lake size (ha), buffer strip width (m), and year of last clear cut: Experiment 1.

Lake	Treatment	Latitude	Longitude	Lake Size	Buffer width	Year of Last Cut
CBL	Buffer	48° 48'	57° 49' 30"	561	18	1991
	Intact	48° 48'	57° 48'	561		
	Clear Cut	48° 48'	57° 49' 50"			
PBP	Buffer	48° 47' 30"	57° 51'	1	13	1991
	Intact	48° 47' 30"	57° 50' 30"	15		
	Clear Cut	48° 48' 30"	57° 51' 30"			
WLL	Buffer	48° 54' 30"	57° 53' 45"	1.25	33	1989
	Intact	48° 54' 30"	57° 54' 45"	16.25		
	Clear Cut	48° 54' 10"	57° 54' 45"			
WBP	Buffer	48° 53' 30"	57° 56' 30"	4.5	14	1990
	Intact	48° 53' 30"	57° 56' 45"	4.5		
	Clear Cut	48° 53' 30"	57° 57'			
GSP	Buffer	49° 18' 15"	57° 33' 30"	125	38	1990
	Intact	49° 48' 30"	57° 32' 45"	44		
	Clear Cut	49° 18' 15"	57° 33' 45"			
BBP	Buffer	48° 52' 45"	57° 56' 30"	1	23	1991
	Intact	48° 52' 30"	57° 57' 30"	7.5		
	Clear Cut	48° 52' 45"	57° 56'			
SAP	Buffer	48° 53'	57° 59' 15"	1.5	36	1990
	Intact	48° 53'	57° 59' 10"	1.5		
	Clear Cut	48° 53'	57° 59' 30"			

Table 2.2. (continued): Experiment 2.

Lake	Treatment	Latitude	Longitude	Lake Size	Buffer width	Age of Last Cut
DP	Buffer	48° 47'	57° 51'	7	24	1991
	Intact	48° 47'	57° 50' 45"	7		
MP	Buffer	48° 52' 45"	57° 45' 30"	25	36	1988
	Intact	48° 52' 30"	57° 45' 30"	25		
PP	Buffer	48° 55' 30"	57° 52' 45"	8	18	1990
	Intact	48° 55' 15"	57° 53'	8		
NP	Buffer	48° 53'	57° 53' 45"	10	33	1988
	Intact	48° 52' 45"	57° 53' 45"	10		
CBR	Buffer	48° 55' 30"	57° 54' 30"	2	na	1991

Table 3.1. Number of artificial tree and ground nests preyed on (percent in parentheses) in riparian buffer strips, intact forest sites, and clear-cut edges in 1996 and 1997.

	1996		1997		Annual Average
Treatment	**Tree**	**Ground**	**Tree**	**Ground**	
Buffer strip	9 (39)	9 (38)	35 (50)	26 (37)	(41)
Intact forest	13 (65)	14 (61)	38 (54)	28 (40)	(55)
Clear-cut edge	17 (71)	13 (54)	30 (43)	23 (33)	(50)

Table 3.2. Results of multiple logistic regression models (G-statistic or deviance) describing the influence of habitat, edges, and buffer strip width on the proportion of artificial nests preyed on. Significant statistics are in bold.

Comparison	Year	N	Model	G (deviance)	df	P
Habitat	1996	90	Lake	8.3	4	0.0799
(Buffer vs. Intact)			Treatment	6.3	1	0.0123
			Nest Type	<0.1	1	0.9508
			Treatment*Type	<0.1	1	0.9043
			Lake*Treatment	**79.3**	**4**	**0.0001**
Habitat	1997	280	Lake	76.7	6	0.0001
(Buffer vs. Intact)			Treatment	0.4	1	0.4880
			Nest Type	**7.0**	**1**	**0.0081**
			Treatment*Type	<0.1	1	0.9054
			Lake*Treatment	**88.5**	**6**	**0.0001**
Edges	1996	91	Lake	**23.5**	**4**	**0.0001**
(Clear-cut vs. Intact)			Treatment	0.0	1	1.0000
			Nest Type	0.9	1	0.3334
			Treatment*Type	1.3	1	0.2467
			Lake*Treatment	6.8	4	0.1143
Edges	1997	180	Lake	29.0	5	0.0001
(Clear-cut vs. Intact)			Treatment	0.0	1	1.0000
			Nest Type	1.6	1	0.2041
			Treatment*Type	0.3	1	0.5575
			Lake*Treatment	**10.7**	**2**	**0.0047**
Buffer strip width	1996/97	268	Width	**15.3**	**1**	**0.0001**

Table 3.3. Percentage of artificial nests preyed on at different lakes and in different treatments in 1996. For lake abbreviations, see Table 2.1. Tree and ground nests are combined due to small sample size (8-10 nests per transect).

Treatment	CBL	PBP	WLL	BBP	SAP
BUFFER	11	50	20	11	90
INTACT	100	88	70	44	13
CLEAR-CUT	89	100	40	40	44
MEAN	67	79	43	32	49
SD	49	26	25	18	38

Table 3.4. Percentage of artificial tree and ground nests preyed on at different lakes and in different treatments in 1997. For lake abbreviations, see Table 2.1.

Treatment	CBL	PBP	WLL	WBP	GSP	BBP	SAP
BUFFER-TREE	0	0	40	60	60	100	90
BUFFER-GROUND	0	0	30	40	60	100	30
INTACT-TREE	10	80	100	10	80	100	0
INTACT-GROUND	30	50	90	10	50	50	0
CUT-TREE	100	20	100	60	10	0	0
CUT-GROUND	60	20	100	40	10	0	0
MEAN	33	28	77	37	45	58	22
SD	40	31	33	23	29	49	35

Table 3.5. Results of the MANOVA type models testing for the difference in concealment on nest types on individual treatments. Significant statistics are in bold.

Treatment	Response Variable	F	df	P-value	r^2
Buffer Strip	Concealment top	1.5	1	0.22	0.01
	Concealment side	**119.5**	**1**	**0.0001**	**0.46**
Intact Forest	Concealment top	1.1	1	0.29	0.01
	Concealment side	**77.8**	**1**	**0.0001**	**0.36**
Clear-cut edge	Concealment top	**18.9**	**1**	**0.0001**	**0.12**
	Concealment side	**112.0**	**1**	**0.0001**	**0.45**

Table 3.6. Logistic regression models (G-statistic or deviance) describing the influences of concealment, the interaction between top and side concealment, and distance to the edge on the proportion of artificial nests preyed on in buffer strips, intact forest (control), and clear-cut edges (n=140 for each). Significant statistics are in bold.

Independent Variables	Buffer Strip			Intact Forest			Clear-cut edge		
	G	df	P	G	df	P	G	df	P
Concealment Top	1.60	1	0.21	0.56	1	0.45	0.06	1	0.81
Concealment Side	1.03	1	0.31	**7.40**	**1**	**0.007**	0.23	1	0.63
Top*Side Concealment	0.16	1	0.69	0.27	1	0.60	0.24	1	0.63
Distance to edge	**8.15**	**1**	**0.004**	**9.90**	**1**	**0.002**	0.04	1	0.84

Table 3.7. Summary of predator outcomes on artificial nests on different treatments and nest types.

Variable	Gray Jay	Red Squirrel	Unidentified Mammal	Not Identified
Buffer strip	6	3	17	27
Intact forest	10	4	14	37
Clear-cut edge	9	9	10	33
Ground	3	6	24	44
Tree	22	10	17	53

Table 4.1. Comparison of number of different-sized eggs preyed on (percent in parentheses) in four buffer strips (n = 80) and five intact forest sites (n = 100).

	Experimental Treatment	
Eggs	**Buffer Strip**	**Intact Forest**
Chinese Quail	19 (48)	26 (52)
Japanese Quail	23 (58)	29 (58)

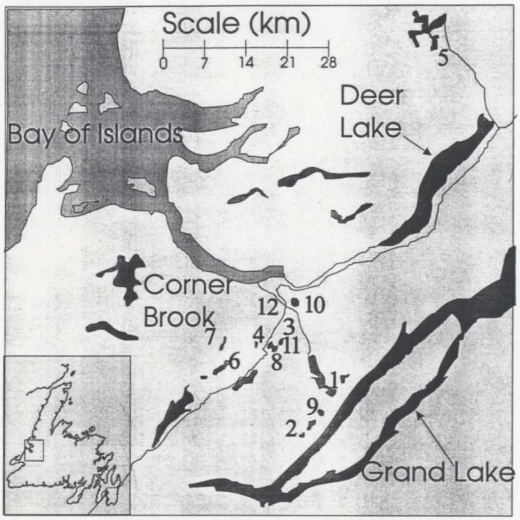

Fig 2.1. Map of study area in western Newfoundland. Numbers indicate approximate locations of study sites (See Table 2.1).

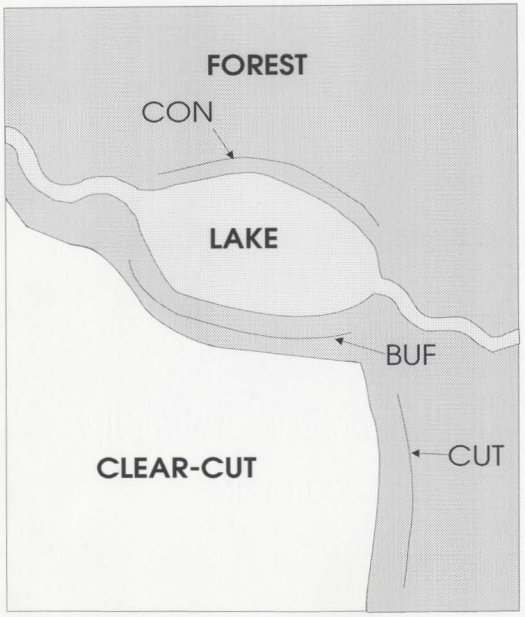

Fig 2.2. General study design. Intact riparian forest = CON, Clear-cut forest edge = CUT, Buffer Strip = BUF

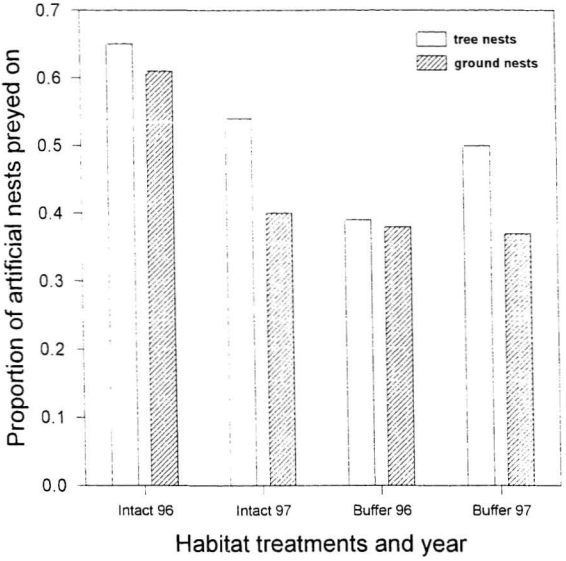

Fig. 3.1. Summary of average proportion of artificial nest preyed on in buffer strips and intact forest.

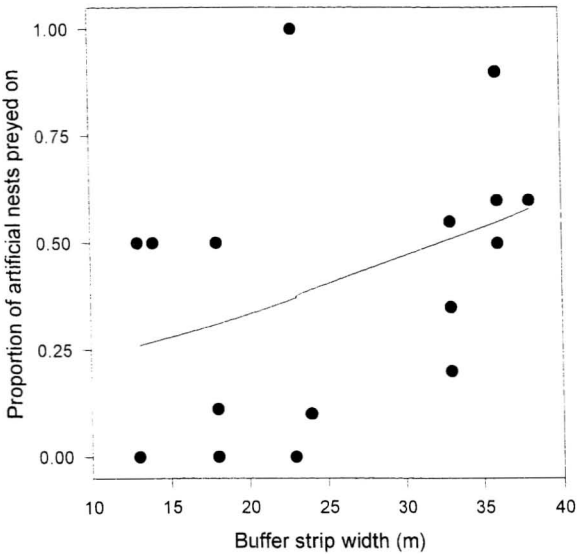

Fig 3.2. The influence of buffer strip width on nest predation. The line represents the predicted value p for the equation $(p/1-p) = e^{(1.79 + 0.055m)}$ where m is meters.

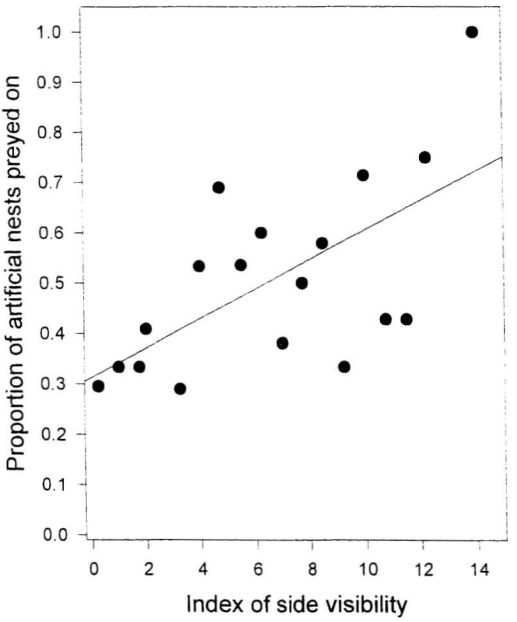

Fig. 3.3. Relationship between visibility from the side and artificial nest predation on all treatments.

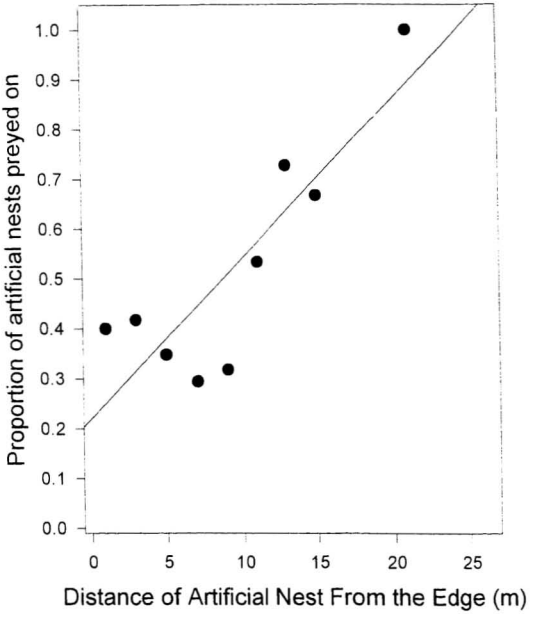

Fig. 3.4. Relationship between distance of the nest from the edge and artificial nest predation on buffer strips.

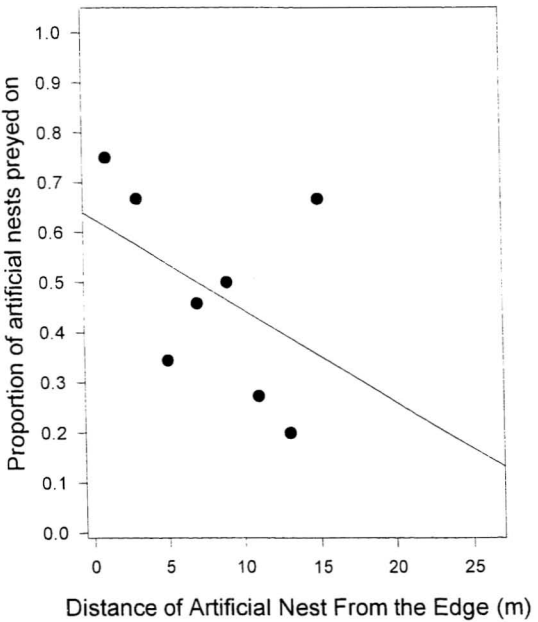

Fig. 3.5. Relationship between distance of the nest from the edge and artificial nest predation on intact forest sites.